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# A REVIEW

OF

# RECENT RESEARCHES

ON THE

# PHYSIOLOGY OF THE NERVOUS SYSTEM.

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"Upon every subject of physiology, and in every stage of our progress in the science, one opinion must be better supported than another; and any opinion—even though in some measure conjectural—founded on the best information which the present state of our knowledge affords, and taken up, not more as a resting-place for the present, than as a stepping-stone to the future, must at least be better than no opinion at all, since it rather invites than opposes itself to further investigation, and, while it spares us much heart-sickening and hopeless confusion at first, often enables us, by working with our previous conclusions in future speculations, to arrive rapidly at truths for which we might otherwise have waited in vain for ever."—*Fletcher's Rudiments of Physiology*, p. 91.

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# INTRODUCTION.

THE physiology of the Nervous System has at all times attracted the attention of men of science, and as it has been a special subject of inquiry by such men as Sir Charles Bell, John Reid, Goodsir, and Bennett,—distinguished pioneers and teachers of biological science in Edinburgh,—it is not inappropriate that it should form, in its more recent development, the matter of this communication to the Royal Medical Society. The reason of this is evidently twofold. *First,* Because in the economy of the body the nervous system is of the greatest importance, as it not only presides over and modifies the actions of all the other systems, but it also is the one which is in immediate relation with the manifestation of those phenomena which are included under the terms Feeling, Emotion, Will, and Intellect. *Second,* Because diseases of the nervous system, are common, are often obscure in their origin and development, are frequently fatal, and add largely to the misery of the human race. It is manifest, therefore, that the more we learn of the functions of the nervous system, the further we will advance in psychology, and in the pathology and treatment not only of nervous diseases, but also of many other maladies in which these functions are more or less affected.

As is always the case in biology, the foundation of an exact knowledge of the physiology of the nervous system is based on correct notions of anatomical structure. For many years anatomists have been acquainted with the general typographical anatomy of the nervous system. In man, the form, size, and relations of the various ganglia, constituting the encephalon and spinal cord, and the course and distribution of the nerves, have been carefully described; but the intimate structure of the nerve centres, as revealed by the microscope, assisted by new methods of hardening, section-cutting, and staining, has only recently come within the domain of exact science. Much still remains to be done in this direction. It is not within the scope of this communication to enter into a detailed account of the researches which have, within the last ten years, been made by many anatomists and histologists in this field, because I intend to limit myself more particularly to the physiology of the nervous system, as elucidated by experimental methods, and I shall therefore only allude incidentally to anatomical and histological inquiry.

The nervous system, as every one knows, is usually divided anatomically into nerve centres and nerves. To these two categories I propose to add a third, namely, the terminal organs of the various sensory nerves. This subdivision, which is correct both anatomically and physiologically, will be adopted in this paper, and I shall now enter upon a description of the advances which have recently been made in our knowledge of the physiology of the nerves, the nerve centres, and of the terminal organs of sense.

## *I.—THE NERVES.*

A nerve possesses at least three distinct properties; 1, that of sensibility, in virtue of which it is capable of receiving a stimulus; 2, that of conductivity, by which it transmits the change produced by the stimulus with a certain velocity; and 3, that of electro-motive force,[1] by which when a transverse section and longitudinal surface are connected with the terminals of a galvanometer, an electric current running from

[1] Electro-motive force is thus defined by Maxwell—"When two conductors, at different potentials, are connected by a thin conducting wire, the tendency of electricity to flow along the wire is measured by the difference of the potentials of the two bodies. The difference of potentials between two conductors, or two points, is therefore called the electro-motive force between them."—*Treatise on Electricity and Magnetism*, by James Clerk Maxwell, &c. &c. Vol. i., p. 47.

the surface of the nerve to its transverse section may be at once detected. We also know that during the active condition of a nerve, that is, while it receives or transmits an impression, there is an elevation of temperature.

1. *Sensibility.*—I am not aware of any recent investigation regarding the sensibility of nerves.

2. *Conductivity.*—Respecting the property of conductivity, or rate of transmission, it is well to remember that, by means of the myographion, Helmholtz, Du Bois-Reymond, and others, have ascertained that in the case of the nerves of the frog, the influence is transmitted at the rate of from 26 to 30 metres per second.[1] According to Schelske,[2] the velocity of the nervous agent in the nerves of man is about 29·6 metres per second. More recently, Helmholtz and Baxt[3] have re-investigated this interesting subject in man. They irritated the median nerve by electrodes, placed first above the elbow and afterwards at the wrist. Contractions were thus produced in the muscles of the thumb, and the difference between the time of these contractions and that at which the nerve received the stimulus, was registered on a plate of glass attached to a pendulum, which, by being interposed in the primary circuit of an induction machine, produced a shock in the middle of its swing. The result of the research is that, in man, the nerve current travels with a velocity of from 35 to 45 metres per second. They also noticed that elevation of temperature increases the rate of nervous conduction. Other two observers, Place and Van West,[4] have repeated these experiments, with substantially the same results.

I now shew you a form of myographion which was employed by Du Bois-Reymond in his earlier researches. The principle of its construction, namely, that at a given moment, it interrupts the primary circuit of an induction machine, and thus, by an induced shock, irritates the nerve, is exactly that of

[1] A metre is equal to 39.37 English inches.
[2] Reichert's Archives, 1864, p. 151.
[3] Monatsbericht der Berlin Acad. 1870, 184.
[4] Pflüger's Archives, iii. 424, 425.

the more complicated instrument of Du Bois-Reymond and Helmholtz. This instrument, termed the spring myographion, is much simpler in construction than the other, and may be rendered quite as exact.[1]

3. *Electromotive force.*—When a portion of a living nerve is placed on the non-polarizable electrodes of Du Bois-Reymond, so that one electrode touches the longitudinal surface while the other is in contact with the transverse section, a current, as manifested by the movement of the needle of the galvanometer, will be found to pass from the longitudinal surface to the transverse section. This may be termed the tranquil nerve current. After allowing the needle of the galvanometer to come to rest, if the nerve be irritated in any way so as to cause a nerve current to pass along it, the needle returns towards zero,—that is, there is always, during a state of activity of the nerve, a diminution in its electromotive power, or what is termed a negative variation. With regard to the tranquil nerve current, it is of importance to decide whether it may not be accounted for by the neurilemma of the nerve tube and the axis cylinder of Purkinje being in different electrical conditions, or, as electricians would say, by these structures having different electric potentials. It would manifestly be a step in advance, if it could be shewn that the neurilemma has nothing to do with the development of electromotive action. This has been done by Morgan.[2] By a very ingenious method, he has succeeded in entirely freeing the nerve tubes from neurilemma, and he has found a current passing as usual from the longitudinal to the transverse section. The question as to the influence of the white substance of Schwann is not so readily disposed of. May not the current be due to different electrical potentials of the white substance and of the axis cylinder? Morgan has also investigated this point. He has found that a current persists, even after the white substance has begun to coagu-

[1] The instrument, with all the electrical connections, was shewn. It is figured, and elaborately described by Du Bois-Reymond, in Poggendorff's Annalen, published since the present paper was read.

[2] Reichert's Archives, 1863, p. 339.

late. I have also myself observed that a current may be readily obtained from non-medullated fibres taken from the sympathetic nerve,—that is, from fibres having no white substance. These facts, conjoined with those obtained by histologists, as to the absence of white substance from nerve-tubes entering nerve-cells or terminal organs, lead one to form the opinion that the axis cylinder is the part specially concerned in conducting nervous impressions. What, then, is the function of the white substance of Schwann? Does it exist merely for protective purposes, or does it act as an insulator of nerve force? That it does play an important part in the economy of nerve is proved by the experiments of Harless,[1] who exposed naked nerves to the vapours of substances having a great affinity for fatty matters, such as oil of bergamot. He found that the vapours acted readily on the white substance, and that there was a consequent diminution of sensibility. The axis cylinder was not affected. If the nerves were placed, after exposure to the vapour, in a warm, moist chamber, sensibility returned. As to the question of the insulating power of the white substance, little can be said. We know that the white substance does not insulate from electrical currents; but possibly it may do so with regard to the mode of energy we term nerve-force.

## *II. THE SPINAL CORD.*

The statements generally accepted with reference to the functions of the spinal cord are the following :—*a*, It contains numerous reflex centres; *b*, Sensory impressions are conducted upwards to the brain by nerve tubes passing through the grey matter near the centre of the cord; *c*, Motor impressions are conducted from the brain to the muscles by nerve tubes passing along the anterior and lateral columns, and also partially through the anterior cornua of grey matter; and, *d*, The posterior columns and the posterior cornua of grey matter are connected with the manifestation of co-ordinated movements. These propositions, since the time of

[1] Molecul-Vorgange, 1. and 2. abtheil.

the elaborate experimental researches of Brown-Sequard, have been generally taught by all physiologists.

### 1. *The Results of Schiff's Researches.*

A series of interesting observations have recently been made by Schiff,[1] by which he has proved that the tubes in the posterior columns conduct tactile impressions. If these columns be cut, there is a complete loss of tactile sensation; but the sense of pain still remains. The loss of tactile sensation is permanent. If all the columns of the cord except the posterior be cut, there is motor paralysis and insensibility to pain, but the tactile sense still remains.[2] These observations are confirmed by the fact, that in *tabes dorsalis,* according to Schiff, where there was loss of tactile sensation, there is usually degeneration of the posterior columns of the cord. But there are cases on record of *tabes dorsalis* in which there was no loss of tactile sensibility. Schiff has also shewn that in the cervical region, above the third cervical vertebra, there is a white band, constituting the respiratory track, composed of nerve tubes, conveying motor impressions to the various muscles of respiration. Section of this part causes complete stoppage of all respiratory movements. By artificial respiration the animal may be kept alive for a considerable period of time; but the injury inflicted by cutting the respiration track is not compensated for by any other part of the cord. It has also been shewn by Schiff, that the lateral grey substance on the right side contains nerve tubes, conducting painful impressions excited in the left posterior extremity, and *vice versâ.* There is thus in man, according to Schiff, a decussation of those tubes; but he asserts that in cats there is no decussation, and that the grey substance conducts painful impressions from the same side of the body. The criticism which I would venture to make on these experimental researches of Schiff is, that the spinal cord of a dog, or cat, or rabbit, is,

[1] Centralblatt, 1872, p. 775.

[2] I cannot comprehend on what data Schiff was able to make this statement, if both motor power and sensibility to pain were removed.

even in large individuals, so very small, that it is extremely difficult to be quite sure that in experiments made on a living animal *so* much is cut, and *no* more. Moreover, it is always a great difficulty in inquiries of this kind to determine how far sensation is affected. After an operation an animal may feel pain, and yet be unable, from motor paralysis, to give evidence of the sensation.

### 2. *Stimulation of the Columns of the Cord.*

Considerable discussion has arisen amongst physiologists as to whether or not the columns of the cord are capable of direct stimulation. Schiff found that the parts conducting painful impressions were incapable of responding to direct stimulation. This statement was first put forward by Van Deen, who distinctly asserted that the anterior and posterior columns of the cord in the frog were not affected by either electrical, chemical, or mechanical stimuli. Guttman, Funke, Sigmund Mayer,[1] Huizinga,[2] Aladoff,[3] and others agreed with Van Deen. Aladoff holds that the posterior columns are irritable, while the anterior are not. Engelken, Sanders Ezyn, and Fick[4] take the opposite view. This question is one which is not so easy to settle as might be imagined; indeed, the array of names known in physiological literature which I have just quoted, indicates at once a difficulty. The difficulty is twofold: (1) That on applying electrodes to the anterior columns, the anterior roots of the spinal nerves may be directly irritated, and muscular movements will follow; and (2), That on applying electrodes to the posterior columns, the posterior roots may be directly irritated, so as to produce reflex phenomena. I have taken many opportunities of examining this problem, and I think it is capable of demonstration that the columns do respond to various stimuli. By using very fine electrodes, so as to touch only a minute portion of the cord mid-way between the points of entrance of the nerves, muscular movements are induced,—not always

[1] Pflüger's Archives, 1868, p. 167. [2] Ibid., iii. p. 81.
[3] Bulletin de l'Academie de St Petersburg.
[4] Pflüger's Archives, 1869, p. 414.

in the part supplied by the nerves near the electrodes, but in in parts supplied by nerves issuing from the cord more posteriorly.

### 3. *Inhibitory Action of Encephalic Centres on Cord.*

Another question in connection with the physiology of the cord, to which I wish shortly to allude, is the following :—Do any of the encephalic centres inhibit or restrain the reflex action of the spinal cord ? We are aware that in the case of the heart the reflex centres may be inhibited,—that is, restrained from action, by irritation of the vagus nerve ; and there are other instances of the same kind of action in the records of physiology. Setschenoff[1] was the first to indicate that the grey matter in the brain of the frog inhibited the reflex action of the spinal cord. The same was asserted to be the case in dogs, after an elaborate experimental inquiry by Simonoff.[2] Another observer, Paschutin,[3] has made a series of experiments on frogs, with the following result :—He found that irritation of the hemispheres of the brain diminished the tendency to reflex action produced by placing a drop of acid on the skin; while the tendency to reflex action excited by gentle titillation appeared to be increased. On decapitation, the tendency to reflex action excited by titillation was diminished. Herzen[4] conducted a series of experiments, under the eye of Schiff, which led him to disagree with the statement that there is any such inhibitory power in the encephalic centres. These researches attracted my attention several months ago. I have repeated several of the experiments made by the observers quoted above. I have not been able to observe the differences between the tendencies to reflex action produced by acids and that produced by titillation. The method I first adopted was, in the first instance, carefully to observe the amount of reflex action excited by a stimulus of definite strength, and, in the next

[1] Ueber die Hemmungs-mechanism für die reflex thätigkeit des Ruckenmarks. Berlin : 1863.

[2] Reichert's Archives, v. 545.

[3] Centralblatt, 1865, p. 794.

[4] Beale's Archives, 1867.

place, to observe whether the same amount of reflex action was obtained by the same strength of stimulus, during irritation of the cerebral hemispheres, by Faradic currents. The results of this method were far from being satisfactory. Sometimes it appeared as if the stimulus applied to the surface of the brain weakened the reflex action, but as often I could detect no effect. I therefore adopted another method, which satisfied me that a strong nervous stimulus transmitted down the spinal cord does restrain the action of certain reflex centres. This method of experiment will be readily understood by one or two examples. On decapitating a pigeon, the body lies, for a second or two, comparatively still, but with muscular tremours. As the cord loses its supply of blood, violent convulsions set in, often so strong as to cause the body to throw somersaults backwards. The legs are stretched out, and the wings flap convulsively. If, during these convulsions, the body be held firmly, and a moderately strong induction current be applied to the upper end of the cord, so as to stimulate it, the convulsions diminish in violence, and may be altogether arrested : on removing the stimulus they recommence. This experiment indicates that a strong nervous current passing down the cord can restrain reflex actions in certain parts of that organ. Another experiment was made, which is even more satisfactory. A pigeon was decapitated, and, with as great rapidity as possible, the posterior wall of the vertebral canal was removed, so as to expose the posterior surface of the spinal cord down as far as the seat of the reflex centres for the legs. Two electrodes of fine wire were now placed over the seat of the reflex centre for the wings, and this centre was irritated by a current so weak as first to cause slight flapping of the wings. Another pair of electrodes was applied to the upper part of the cord, and it was found that a stronger stimulus at this portion of the cord at once stopped the movements of the wings. This proved that the nerve current produced by the electrical stimulation at the upper part of the cord, when it passed down the cord, was capable of restraining the reflex nervous action produced by gentle irritation of the posterior columns and probably of the posterior roots of the spinal nerves. These experiments do not indicate the encephalic centre which is capable of restraining these movements. I have failed in observing any movements following Faradization of the cerebral hemispheres of birds. As there are good grounds for believing that many of the actions of birds are reflex, such as the movements of the wings during the long flights of migratory birds, it is possible that the reason why no movements occur on Faradization of the cerebral hemispheres, is, that the stimulus may simply restrain these reflex actions, and consequently we have no movements similar to those observed on Faradizing the convolutions of the brain of a mammal. These observations also assist in the explanation of how it is that we are able, by a strong effort of the will, to restrain in a great measure reflex actions excited by titillation, &c. It may be objected to this view, that when we will to restrain movements, there may be a direct restraining action in the muscles involved, or on antagonistic groups of muscles. The first supposition involves the theory that there are two sets of nerves for each muscle,—one for causing it to act, and the other for preventing its action. Of this there is no proof. The other supposition is negatived by the fact, that antagonistic groups of muscles are not in a state of contraction during an effort of the will. It appears to me that the facts are better explained by the theory, that certain encephalic centres may have a restraining or inhibitory power over spinal centres.

## *III. THE ENCEPHALON.*

In no department of physiological research has more interest been lately excited, than in the discoveries which have been made recently regarding the functions of the brain by investigations in France, Germany, and Great Britain. Almost as if by a series of combined efforts an assault has been made upon this difficult subject. Already the outworks have been carried, and we are pressing toward the citadel. It is my purpose now to give such an account of the result of these investigations as will be readily understood. As all are aware, the old method of investigating the physiology of the nervous centres in the head, was by vivisection. Magendie, Flourens, Matteucci, Longet, Schiff, and many others practised the method of operating on the brain by removing certain portions, and by afterwards noticing the effects produced. Perhaps the last inquiry of this kind which may be made[1] was conducted by myself, and the results were recorded in a paper read before the Royal Society of Edinburgh on 6th January 1873. Since then new methods of inquiry have been employed, and I shall now classify and describe the results of these as follows:—

## *A.*—Method of Removing a Portion of Brain in Adult Animal, and observing the effects.

In the summer of 1871, I began a series of experiments on pigeons. These were continued, with intermissions, up to the month of July 1872. Pigeons were chosen because I wished to repeat the observations of Flourens and others, who had performed numerous well-known experiments on these birds. I found, moreover, by experience, that other animals—such as rats, rabbits, monkeys, frogs, &c.—rarely survived the operation a sufficient length of time to warrant me in making trustworthy observations.

### 1. *The Mode of Experiment.*

This consists in removing, under chloroform, a portion of the brain, and observing the effects produced. In order to give as great a degree of precision as possible, it is necessary, in the first place, to study the anatomical relations of the parts concerned. This I have done, and now feel tolerably confident I can remove the grey matter corresponding to the cerebral hemispheres without materially injuring the *corpora striata.* Those structures blend together anteriorly and

[1] Recent observations of a similar character have been made by Goltz (Centralblatt, 1868, p. 690 and p. 705), Voit (Münich. Akad. Bericht, 1863 and 1868), and by Rosenthal (Centralblatt, 1868).

laterally to such an extent, as to render it impossible to remove the cerebral hemispheres without severing the bond of connection; but the cerebral hemispheres, represented by a thin layer of grey matter, constitutes so small a proportion of the prosencephalon, that practically they may be entirely removed, while the corpora striata are left intact, except along the line where they merge into the hemispheres. The same operation cannot be so satisfactorily performed on any mammal. The difficulties in the way of obtaining trustworthy results in these experiments, are chiefly that they may be complicated by, first, the effects of shock; and, second, by the effects of hæmorrhage. These effects cannot be avoided; and, therefore, in no case have any trustworthy observations been made until from twenty-four to thirty-six hours after the operation. It is surprising how soon a pigeon rallies from the effects of a formidable operation on the brain. I have often seen a bird taking food within twenty minutes after one cerebral hemisphere had been removed. I have always operated when the bird was under the influence of chloroform, from a desire to avoid, as far as possible, unnecessary pain. The effects of the chloroform, however, are not unfrequently to cause vomiting and consequent hæmorrhage. In order to reach the brain, I first made a longitudinal incision along the median line of the scalp. The scalp is pushed aside with the fingers, so as to expose a portion of the cranium. With a pair of sharp strong scissors, a part of the roof of the cranium is readily excised, the size of the piece varying according to the extent of brain which it is desirable to remove. The cerebral substance is cut with a very sharp knife. There is usually considerable hæmorrhage. The scalp is quickly brought over the wound, and a little cotton wool placed along the line of incision. A clot forms, and the bleeding is arrested. The wound heals rapidly. It is necessary, after the first twenty-four hours, to feed the birds frequently, by introducing food in the form of grain, or barley, or peas, when it is immediately swallowed by the reflex mechanism of deglutition. The operation of removing the right or left cerebral hemisphere is not usually fatal. There is, in the next place, a marked contrast between the fatality following the removal of the anterior and that following the removal of the posterior portions of the hemispheres. When the anterior portion was removed, in ten, eight recovered; while only three recovered when the operation removed the posterior portion. The probable cause of this difference in the mortality is twofold: 1st, Birds from which the posterior lobes have been removed rarely feed themselves; and 2d, when the posterior lobes are removed, severe hæmorrhage is apt to ensue, and blood to be effused on the surface of the medulla. Removal of both hemispheres is attended by about the same fatality as removal of the posterior portion. Removal of both hemispheres, with the upper portions of the corpora striata, is a serious operation; but in one fortunate instance the bird survived till the two hundred and twenty-fourth day. It is to be observed, however, that this operation was usually attended by only partial recovery, inasmuch as after the shock had been recovered from, and the wound had healed, nutrition was carried on imperfectly, and the bird slowly declined in strength and vigour. The general conclusions from these facts are, that the mortality following operations on the brain of pigeons increases in proportion as the deeper portions are affected; and that when injury is done to the deeper layers of the corpora striata, the result is death, often immediate, but always within three days from the time of the operation.

Among other effects I shall notice the following:

### 2. *Effects of Removal of Cerebral Hemispheres on Vision.*

Numerous experimenters have found, that when the upper part of the brain of a pigeon is removed, the bird loses the sense of vision; but none have endeavoured precisely to state how much was removed, nor have given a satisfactory explanation of the result. The question, whether a bird has lost the sense of vision, is more easily tested than the equally important one of how far the other senses are affected;

because it is easy to blindfold one eye by placing a small bit of plaster over it, and to apply tests to the eye under examination.

With special reference to the function of vision in this research, I have found—

*a.* That removal of the anterior part of both hemispheres does not interfere with vision.

*b.* That removal of the posterior part of both hemispheres does not interfere with vision.

*c.* That removal of one cerebral hemisphere, either the right or left, is followed by loss of vision on the opposite side.

That removal of the anterior or of the posterior portion of both hemispheres does not affect the sense of vision, is a recognised fact, which can only be explained on the supposition that the faculty of the consciousness of sight is not located in one or the other portion. But there is great difference of opinion amongst physiological writers as to whether there is any sensation after complete removal of the cerebral hemispheres. The term "sensation" is very vaguely used by many writers, and much confusion has arisen in consequence. It is quite erroneous to call the change in the nerve centre, which is one of the essential conditions of a reflex action, a sensation. This mistake, however, is often made. The meaning I attach to the term is expressed in the well-known definition: "Sensation is the consciousness of an impression." I do not understand how it is possible to have any sensation without consciousness—that is, to feel without being aware of it.[1] But the acuteness of conscious perception

[1] I find it quite impossible to conceive the idea of "unconscious sensation," as has been suggested by several physiological and psychological writers. Any nervous change of which the "Ego" is unconscious cannot possibly be a sensation; because the word, in the sense usually employed, expresses a change in the "Ego" consequent on some change or other in that which is not the "Ego." It appears to me, also, that even those who regard the "Ego" as a metaphysical abstraction expressing the result of the highest kind of nervous action in cerebral centres, must have the same difficulty, because the phenomenon termed by them a sensation cannot be *proved* to occur except during action of the cerebral centre. The only

may vary. We may be conscious in certain circumstances, as in awakening from sleep, of the presence of light, without having any definite ideas or images associated with the sensation. We may have a sensation, followed by no ideas, attended by no images of external objects (or revived sensations), and resulting in no act of volition or emotion. Majendie, Longet, Dalton, and others, appear to think that a certain amount of sensation exists after removal of the cerebral hemispheres, and they locate these sensations in the ganglia at the base of the brain. While observing the results of my earlier experiments, I was inclined to adopt the same view, because birds perform many actions after ablation of the hemispheres, which it is difficult on first thoughts to account for, unless on the supposition of the persistence of a certain degree of sensation. But later experiments, and more especially those in which I removed one cerebral hemisphere along with the upper part of the corresponding corpus striatum, seem so clearly to indicate that consciousness or sensation has its seat in the cerebral hemispheres alone, that I have no doubt on the matter. In thirty-eight birds, eight had the right hemisphere, eight the left hemispheres, ten the right hemisphere and upper part of the right corpus striatum,

legitimate test of the question must be applied in the case of a being who can positively say, in a given experiment, whether or not on a peripheral irritation he experiences a sensation. The movements of the legs of a decapitated frog do not constitute evidence of sensation; while, on the other hand, the movements of the limbs of a man who, while in full possession of all his percipient and intellectual faculties, has his spinal cord so injured as to prevent the transmission of impressions between the brain and the limbs, prove that there may be movements without any sensation whatever. These points are discussed in the following works: Haller's Physiology; London, 1754; Chapter on the Brain. Anatomy and Physiology of the Human Body, by John & Charles Bell—"Introductory View of the Anatomy of the Brain." Fletcher's Rudiments of Physiology; Edinburgh, 1837: Chapter "On the Nature of Sensation." On Intelligence, by H. Taine; Book III. Of Sensations. Problems of Life and Mind, by George Henry Lewis; 1874; Biological data, p. 128. Harris' Journal of Speculative Philosophy; St Louis. Mo. 1872—Article by John C. Thompson on "Empirical Certitude." Also in the works of Herbert Spencer, Bain, and Maudsley. The question is also ably argued in a "New Theory of Knowing and Known," by John Cunningham, D.D., 1874, p. 83 *et seq.*

and ten the left hemisphere and upper part of the left corpus striatum, removed, and in every instance there was blindness on the opposite side. This was tested by careful experiment. For example, after allowing any of these birds to settle in one position, and blindfolding one eye, it was not difficult to determine whether or not there was any consciousness of vision on bringing a rod suddenly near the other eye. If the bird saw, it started away; if it did not see, it remained motionless. In the case of birds which had the hemisphere removed without materially injuring the corpus striatum there still appeared to be a dim perception of light, inasmuch as the bird started suddenly to the side when a brilliant light was brought near the eye. When the light was on the floor, and the pigeon placed near it suddenly, it would avoid the flame, when I attempted to push it in that direction. A bird, on the other hand, from which not only the hemisphere, but also the upper part of the corresponding corpus striatum had been removed, was quite passive when the blind eye was brought near a flame; and when rapid movement was made opposite the sound eye, it would go sideways into the flame. The first difficulty here is to distinguish a conscious from a reflex action, and different interpretations may be put on the facts I have just narrated. My own impression is, that in those cases in which there is apparently a degree of consciousness after the supposed removal of the cerebral hemisphere, a portion of it is still left, because when to give certainty to the result, a portion of the corpus striatum is also removed, I have observed no indication of consciousness whatever. It is impossible to draw the boundary between the corpus striatum and the cerebral hemisphere. Whether or not there is a vague kind of consciousness in the upper part of the corpus striatum of a bird where it blends at its outer and anterior part with the cerebral hemisphere, is doubtful; but my experiments clearly show that the optic lobes do not manifest the phenomena of consciousness. My conclusions differ *in toto* from those of Majendie, Longet, Vulpian, and Dalton, who assert, that if an incision be made between the tubercles and the cerebrum, or if the cerebrum itself be taken away while the tubercles are left untouched, vision still remains. I have found quite the contrary. All my experiments prove that removal of one hemisphere, or of one hemisphere and the corresponding corpus striatum, is attended by blindness on the opposite side. In those cases a *post-mortem* examination shewed that the optic tracts and optic lobes were uninjured. A microscopical examination of the retinæ, in one case, shewed that both were alike normal. The optic lobes were also examined, and were found in a healthy condition, and exactly alike. The optic nerves and optic tracts were also normal. The inference, therefore, is that the apparatus for conscious perception was alone wanting. Light from objects placed before eye on the blind side excited the retina, and the iris remained contractible; the optic nerve conducted an influence from the retina; the optic lobe performed its functions, whatever they may be; influences were transmitted upwards towards the hemisphere, but there was no hemisphere to receive them, and consequently no consciousness. From these considerations it appears that, for the conscious perception of external objects by vision, we require—1*st*, a sense or terminal organ, the retina; 2*d*, a nerve, the optic nerve; 3*d*, an optic lobe; and 4*th*, a cerebral hemisphere. The optic lobe does not appear to me to be the seat of sensation. When the optic lobes are injured, the animal staggers, runs to the side (describing a semi-circle), and finally falls over on the side opposite to that on which the injury was inflicted. Consciousness is never affected. There are no convulsions, unless the *crura cerebri* are accidentally injured. There is blindness on the opposite side.

When we consider how intimately associated the sense of sight is with the combined movements of the limbs, the disturbance of motion after injury to the optic lobes may be readily accounted for. Any interference with the vision of a healthy pigeon will produce movements of the same kind. Motion in man, such as walking, may be voluntary, or altogether reflex in character. When the cerebrum is occupied with a succession of thoughts bearing no relation to surrounding circumstances, we walk without being conscious of directing our steps, and still we avoid an obstacle, or take a longer or shorter step as may be required. An individual in a somnambulistic state is not conscious of a light placed before his eyes, but he will avoid walking against it. These are examples of reflex actions, the mechanism being—1*st*, the retina, which receives the influence of light and affects the optic nerve; 2*d*, the optic lobes which are the centres of reflex action; and 3*d*, motor nerve tubes passing from these lobes to the corpora striata, and from thence to the anterior columns of the spinal cord. When we consider the relative large size and structural complexity of the optic lobes in birds, we must regard them as important reflex centres of the kind alluded to.[1] Hence many of the motions of birds may be regarded as purely reflex, and altogether unconnected with consciousness. In the higher animal (and more especially in man), movements are commonly guided by cerebral action, and the reflex action of the optic lobes is not called into play. Hence in these, the optic lobes are smaller and less complicated in histological structure.

The optic lobes may therefore be regarded as the encephalic centres of vision for receiving influences from the retina, and transmitting these to the cerebral hemispheres; or they may act as reflex centres, producing movements which are co-related with vision. In the same manner each sense has probably its encephalic ganglion; but with the exact position of these, such as those of taste and hearing, we are at present unacquainted.

### 3. *Effect of Removal of the Posterior Half of both Cerebral Hemispheres.*

Removal of the posterior half of both cerebral hemispheres is marked by only one feature, namely, the birds are unable

[1] It may be here objected that in those cases in which the pigeon had one cerebral hemisphere removed, reflex movements did not follow the act of placing a light before the eye on the opposite side. It is difficult to account for the fact, or to harmonise it with the well known results obtained in the case of the somnambulist. It is quite possible the operation may have interfered in the case of the bird with the reflex mechanism, which is intact in the sleep-walker.

to feed themselves. They are evidently hungry, and go about pecking at corn and barley, but they always miss the grain, and frequently they do not open the beak. This feature is most marked about two weeks after the operation. About that time they succeed occasionally in catching the grain, and after some practice, they become able to feed themselves as other pigeons do. These facts would seem to indicate some want of co-ordination between vision and voluntary muscular movement.[1]

### 4. *Effects of Removal of the Cerebral Hemispheres without materially injuring the Corpora Striata.*

Removal of the whole cerebral hemispheres without inflicting much injury on the corpora striata, is followed by a loss of intelligence and sensation. Motion is still perfect. If thrown into the air the bird can fly, and occasionally it will walk about. The question is, Is the loss of intelligence and sensation absolute? The probability is, that in those cases in which there still appears to be a certain amount of intelligence and sensation, a small portion of the cerebrum is left. On one occasion I observed a bird, from which I thought I had removed all the hemispheres, try to avoid another, and even to peck it. On examining the brain of this bird after death, I found that a small portion of the anterior part of the right hemisphere still remained.

In the case of the bird that survived 224 days, and from which I had removed the cerebral hemispheres and upper part of both corpora striata, I observed one evening the following incident:—I threw it into the air in my study; it flew about for a minute or so and then attempted to alight on the back of a chair, but the chair was unsuitable for a firm resting place. The bird slipped, struggled, and fell to the floor. I picked it up and again caused it to fly, with a similar result. This I repeated a third time, but on this

[1] This curious result may also now be partially accounted for by supposing that the operation of removing the posterior half of both cerebral hemispheres would be very likely to injure the cerebellum, either directly or by subsequent implication.

occasion it hovered over the back of the chair for half a minute, in vain attempting to alight, when it turned round and flew to the top of the door of the room, which was half open; there it rested securely. Now, in this case, I examined the brain very carefully with the view of ascertaining whether any cerebrum remained. I found none, but it is quite possible that part of what I called corpus striatum, at the outer edge of the encephalon, might have been a minute portion of a cerebral hemisphere.

### 5. *Effects of Removal of the Cerebral Hemispheres, along with upper half of the Corpora Striata.*

Removal of the cerebral hemispheres, along with the upper half of the corpora striata, causes loss of intelligence, volition, and sensation. There is no loss of the co-ordination of movement, neither is there paralysis. This is only in the case of birds. In rabits, dogs, cats, rats, and monkeys, injury to the corpora striata causes paralysis; but in pigeons there is none unless the deeper parts of the bodies are injured. A bird from which the hemispheres and upper parts of the corpora striata have been removed, is in a state of profound stupor, from which it cannot be aroused. When a loud sound is made near it, or a brilliant light placed quickly before its eyes, it may start, turn its head, yawn, but drawing its head deeply down on its breast, it relapses into a motionless condition. It manifests no fear. It shews no excitement when placed beside a cat. When immersed in cold water, there are at first a series of flutterings, but in a minute or two the bird passes into its usual condition. It occasionally walks, and if it come to the edge of a table it steps over, and falls helpless on the floor. I am convinced all its actions are reflex, not associated with consciousness.

### 6. *Effects of Injuring the Deeper Portions of the Corpora Striata.*

Injury to the deeper portions of the corpora striata is followed, first, by severe convulsions, and afterwards by paralysis of both extremities. The animal soon dies, rarely living more than three days after the operation. No convulsions are produced by pricking, cutting, or irritating the upper part of these bodies, but when the needle or knife is passed to the base, convulsions, often violent, are produced. I have never succeeded in removing the whole of the corpora striata without an almost instantaneously fatal issue. I cannot therefore agree with the observations of the distinguished French physiologists, Longet and Vulpian, who state that animals (even mammals) survive after complete removal of the hemispheres, corpora striata, and optic thalami. The explanation of the difference between us probably is, that the distinction between cerebral hemispheres and corpora striata has not been sufficiently attended to by them, for my experiments shew that the deeper part of the ganglia, which I hold to be homologous with the corpora striata, cannot be removed from pigeons without a rapidly fatal result.

### 7. *General Result as to the Functions and Homology of Corpora Striata in Birds.*

The results of these physiological experiments I will now briefly sum up as follows :—

1. The ganglia, termed the corpora striata in birds, are not strictly homologous with the same bodies in mammalia. Each body consists in its deeper layer of a mass of nervous matter (in immediate connection with the crus cerebri), which represents the true corpus striatum of mammalia. The layer of grey matter forming its upper and outer part, and which blends with the thin grey layer representing the cerebral hemisphere, is properly to be regarded as part of the latter. In a bird, the upper parts of the corpus striatum and the cerebral hemisphere present the same structure, and physiological experiment appears to indicate that their function is also the same. Removal of the upper gray layer, along with the upper part of the corpus striatum, is attended by a like result, loss of sensation. This is not the case after experiments on rabbits, cats, dogs, rats, or monkeys. In these animals injury to the *upper* part of the corpora striata always affects not only sensation, but also motion, paralysis

being produced. This is corroborated by the well-known effects of apoplectic effusions in man.

2. In pigeons, the ganglia, usually termed the corpora striata, are double organs, and have a twofold function: *a* The lower, or deeper part, is concerned in motion; *b* The upper part is that in which changes occur which give rise to sensations which are not associated with images, and are ill defined.

*a*. That the deeper portions of these ganglia constitute the centre from whence emanate many of those nervous influences which occasion contraction of the muscles is, I think, clearly indicated by the fact, that irritation of these parts produces violent spasmodic contractions of groups of muscles, while their destruction at once produces complete paralysis.

*b*. It is more difficult to establish the point that the upper parts of these bodies are the seat of crude, ill-defined sensations. I have found on carefully removing the upper layer of grey matter (usually called in pigeons the hemisphere), without materially injuring the ganglia underneath, that the bird, though in a dull, stupified condition, still sees and avoids a threatened blow. It is not, however, easy to demonstrate, as I have before remarked, that in such cases the whole of the cerebral portion has been removed. But when the upper parts of the ganglia underneath are also removed, the bird passes at once into a state of profound stupor. In the first case, enough of grey matter was doubtless left on the surface of these ganglia to be the agent of indefinite sensations of light, sound, &c., but the part of the grey matter which would have added to these sensations associated images, such as those of relief or distance, was wanting. The changes which occur in the upper layers of the corpora striata, result in bare sensations, without being associated with memory, forethought, or judgment, and all the assemblage of emotions, desires, fears, and determinations developed by the notion of approaching danger, or of future pleasure. These latter phenomena, in so far as they can occur in a pigeon, require for their manifestation the thin layer of grey matter stretching over the ganglia, which is usually considered as the homologue of the cerebral hemispheres in the higher animals. I hold that this layer represents only the upper layers of the convolutions in man, and that the grey matter found over the ganglia in birds, more especially antero-laterally, represents the deeper layers of the cerebrum of man.

### *B.*—Method of Electrical Stimulation of the Surface of the Brain.

The method of research by vivisection is open to many objections, the chief of which is, that the severity of the operation and the loss of blood may cause such a state of shock, as to vitiate any inferences that might be drawn from the facts recorded. A new method, however, has been devised, namely, that of stimulating the nervous centres by electricity, and observing the results. Until recently, it has been accepted by all physiological authorities, that the cerebral hemispheres are destitute of irritability. It was apparently shewn by Longet,[1] Majendie,[2] Matteucci,[3] Weber,[4] Budge,[5] Schiff,[6] and others, that irritation of the surface of the hemispheres called forth no muscular movements.[7] It was consequently concluded that the cerebral convolutions over their entire extent were associated with the phenomena of the mind. The method of irritating the surface of the brain, with a weak galvanic current, was pursued in Germany by Fritsch and Hitzig conjointly, who obtained by means of it certain definite results; and in England, by Ferrier, whose researches have been much more extensive, and from their relation to pathology, much more important.

[1] Anatomie et physiologie des systéme nerveux de l'homme et des animaux vertébrés. Paris, 1842, T. I.

[2] Leçons sur les fonctions et les maladies et de nerveux. Paris, 1839.

[3] Traites des phénoménes electro-physiologique des animaux. Paris, 1843.

[4] Wagner's Handwörter-buch der physiologie. Bd. iii.

[5] Untersuchungen über das nerven system. Frankfort, 1842.

[6] Lehrbuch des physiologie des Menschen. 1859.

[7] For an admirable review of those experiments see Report by W. B. Neftel, M.D., in Brown-Sequard's and Seguin's Archives. New York, No. 5. 1873, p. 380 et seq.

1. *The Method and Experiments of Hitzig and Fritsch of Irritation of Surface of Brain by interruptions of a Continuous current.*

The commencement of this method of inquiry dates from an observation made by Hitzig on a wounded soldier, during the Franco-Prussian war, that galvanic irritation of a portion of the cerebral hemispheres excited contractions of the muscles of the orbit. Experiments on the lower animals were begun by Hitzig and Fritsch when peace was restored.[1] The method was very simple. A portion of the calvarium was removed from dogs, the sensitive dura mater was slit up and carefully removed from the surface of the convolutions, and areas on these were then irritated by a weak continuous current. The results of these inquiries may be briefly stated as follows :—

1. In the anterior portions of the surface of the hemispheres, there are certain definite regions, irritation of which causes muscular movements on the opposite side of the body.

2. Irritation of the posterior lobes produce no muscular movements.

3. The centre for the muscles of the nape of the neck is in the middle of the prae-frontal convolution.

4. The centre for the extensor and adductor muscles of the anterior extremity is situated at the external end of the post-frontal convolution, and a little behind this is the centre for the flexor and rotator muscles of the same limb.

5. The centre for the muscles of the posterior extremity is placed also in the post-frontal convolution, but posteriorly and internal to the centre for the anterior extremity.

6. When a continuous current is allowed to flow through the brain, the irritating influence is chiefly in the neighbourhood of the positive pole.

7. The irritability of the brain is rapidly diminished by hæmorrhage, and the convolutions cease to respond to electrical stimulation long before the nerves cease to be affected.

[1] Ueber de electrische Errebarkeit des Grosshirns. Reichert and Du Bois-Reymond's Archives. 1870, p. 300.

8. The effects just described cannot be due to irritation of the ganglia at the base of the brain, which are well known to be connected with motion; because, (1.) the current employed is (*a*) so weak, and passes (*b*) through such a short distance between the electrodes; and (*c*) the resistance of brain substance is so great that the current cannot reach the deeper parts; and (2.) the muscular contractions stop when the electrodes are slightly shifted.

9. The removal of the portion of the convolution acting as a centre did not cause complete paralysis of the muscles with which it was associated. For example, Fritsch and Hitzig removed the centre for the muscles of the fore limb. The limb was not entirely paralysed, but the muscular sense was abolished. [Compare with result of Nothnagel's experiment, p. 33.]

### 2. *The Method and Experiments of Ferrier, by Irritation of Surface of Brain by a weak Faradic current.*

Dr Ferrier's[1] researches were made in the first instance, in the pathological laboratory of the West Riding Asylum, and afterwards in the laboratory of the Brown Institution, London. In the month of August last, through the kindness of Dr Ferrier, I had the opportunity of seeing a repetition of many of these experiments. The demonstration was most satisfactory and convincing. Dr Ferrier has experimented on pigeons, fowls, guinea-pigs, rabbits, jackals, and monkeys. The method of experiment is that already described as the one pursued by Fritsch and Hitzig. The irritating current was derived from the secondary coil of Du Bois-Reymond's induction machine, the primary coil of which was in connection with one Stöhrer's cell (with carbon and zinc elements). By moving the secondary coil in the sliding board, and thus increasing or diminishing the distance from the primary coil, the strength of the current

[1] The West Riding Lunatic Asylum Medical Report, Vol. iii. p. 30. British Medical Journal, April 1873, p. 457. Turner and Humphrey's Journal of Anatomy and Physiology, No. XIII., Nov. 1873, p. 152.

may be carefully graduated. Dr Ferrier has observed the following phenomena :—

1. Stimulation of the surface of the hemispheres causes a determination of blood to the part stimulated.

2. Stimulation of areas on the surface of the anterior lobes of the hemispheres causes muscular movements on the opposite side of the body.

3. Long continued Faradization causes convulsions of an epileptiform character. The convulsions were always preceded by "an excited hyperæmic condition of the cortical matter of the hemispheres."

4. As regards the presence of motor centres in the cerebrum, the two sides of the brain are completely symmetrical.

5. Irritation of the posterior lobes, or of the gyrus fornicatus, is not followed by muscular movements.

6. In certain animals the centres for special movements are more differentiated than in other animals, in a manner corresponding to the habits of the animal. Thus, the centres for the lips of the rabbit, the tail of the dog, and the paw of the cat, are highly differentiated.

7. The application of electrodes to the corpus striatum in the dog caused pleurosthotonos, and the flexors of the limbs were strongly contracted.

8. Irritation of the anterior tubercles of the corpora quadrigemina caused opisthotonos and extension of the limbs, and the action was, as in the last case, a crossed one—that is, irritation of the left tubercle caused violent extension of the muscles of the right side of the body, and *vice versa*. There was also dilatation of the pupil.

9. Irritation of the cerebellum causes movements of the muscles of the eyeballs, and each lobe of the cerebellum acts as a centre for alterations of the optic axis.

10. Epilepsy consists essentially of a series of discharging lesions of the different centres in the cerebral hemispheres; while chorea is of the same nature as epilepsy, and depends on momentary discharging lesions of the individual cerebral hemispheres.

These experiments and observations are important, both to physiology and pathology. Conducted by one who is thoroughly competent, by long and careful educational training for such work, these researches have, during their progress, been rigidly scrutinised by many keen observers. There can be no difference of opinion as to the facts made out by Faradization of certain areas of the surface of the brain. There will be no doubt much controversy regarding the interpretation of these facts. Many speculations are at once suggested. I can only refer to one,—namely, What is the relation between these motor-centres and those other centres which are more immediately related to mind? Ferrier is of opinion, from the fact that there is an intimate relation subsisting between thought or ideation and the outward expression of the idea in muscular action, that there is a close anatomical association between the ideational and the voluntary motor-centres. Thus, he says:—"I should incline to the opinion, that the organic centres of word memory are situated in the same convolutions as the centres which preside over the muscles concerned in articulation. If this be so, then we ought to have a hand memory, a face and eye memory. And thus we may ultimately be enabled to translate into their physiological signification, and localise phrenologically the organic centres of various endowments."[1]

It has always appeared to me, in connection with these researches, an interesting speculation, to account for the normal stimulus which acts, let us say, on the motor centres, regulating the movements of the arm of a monkey, when it

[1] Since the above was written, objections have been urged by various physiologists to the inferences drawn by Ferrier from these experimental facts. It is still urged that there is no absolute proof that the nervous influence causing the muscular movements originates in the part of the surface of the brain to which the stimulating electrodes are applied. It is possible the influence may be diffused, and it is also highly probable that a change in the electrical condition of one portion of the brain will excite a change in the electrical condition of an adjoining portion. This change in the electrical condition of the second portion may, as in the familiar experiment of Matteucci's induced contractions, be quite sufficient to stimulate nerve tubes in connection with it. Of all this, however, there is no proof, and the fact that on stimulating certain areas on the surface of

stretches it forth to grasp an apple. When the animal is deeply under chloroform, with its brain exposed, Ferrier can, by a gentle Faradic stimulation, cause the monkey to put forth its arm with a number of such complicated movements as it would make to seize an apple. Here the stimulus is the Faradic current; but what sets the mechanism in motion in normal circumstances? What is the stimulus to the motor centre then? The stimulus must come from somewhere, and probably, one would conjecture, from another centre, say in the posterior lobe, which would be a psychical centre in close physiological relationship with the motor centre. But what energy will set the physical centre into action? Must we here call in the action of an "Ego," manifested as Will, or can the stimulus in any way be accounted for by the application of some physical mode of energy? If we call in the action of the former, nothing is explained. The stimulus to this psychical centre is, in all likelihood, derived from that furnished by impressions on the senses, such as that of sight and smell. The sense-impression conveyed to the brain may be supposed capable of setting the nervous mechanism in motion in a manner analogous to the action of a trigger.[1]

### *C.*—Method of Local Destruction of a minute part of the Nervous Matter on Surface of Brain.

While Fritsch and Hitzig and Ferrier were thus pursuing their researches, another German physiologist was investigating the matter by an entirely different method.

the brain, either by an interrupted galvanic current, as has been done by Hitzig and Fritsch, or by a Faradic current, as has been done by Ferrier, certain movements follow, the same in character in various experiments, is a decided advance in science. That these facts are to revolutionise all our notions, or to form the basis of a new cerebral physiology, or to add more of certainty to the inductions of phrenology, are hopes which will certainly prove very disappointing to any who may have cherished them.

[1] On this subject the reader may consult, with advantage, an article in the *British Quarterly Review* for January 1874, on "Mind and the Science of Energy," in which all the modern aspects of the problem of the relation of mind to matter are discussed.

Nothnagel's[1] method is to make an incision on a rabbit's head; the skull is then bored through with a short sharp needle, taking care not to injure the brain. Through the opening thus made, a drop (about $\frac{1}{4}$ to $\frac{1}{2}$ of a medicinal drop) of concentrated chromic acid is injected by means of a hypodermic syringe, having a very fine canula. The wound is then closed. At first little or no effect is observed. There is no hæmorrhage, and no exposure of brain surface. The intracranial pressure remains normal. The animals live for a period of from a few hours to three weeks. After death, a minute, resistant, hard, green portion of the brain is found surrounding the spot where the chromic acid was injected. By means of this method, among other results, Nothnagel has found that, when the chromic acid lesion affected the outer end of the post-frontal convolution, there was a complete loss of the muscular sense of the opposite fore-extremity. This area on the post-frontal convolution is that indicated by Fritsch and Hitzig, and by Ferrier, as being the seat of the centre for the anterior extremity. The paralysis of the muscular sense, however, was not persistent, but disappeared in from six to twelve days. Reasoning on his experiments, Nothnagel holds that the localities in the cortical portion which he has injured do not contain the terminations of nerve tubes which proceed directly from thence to the muscles; but that they are merely intermediate stations, and that other routes may conduct the orders of the will to the same muscles. The method pursued by Nothnagel is one likely to be useful in endeavouring to determine the effects of minute local injuries to the brain, an inquiry which might be expected to lead to important results in nervous pathology.

### *D.*—Method of Removing a Part of Brain, or of Cutting a Nerve after Birth, and observing the effect on the adult condition.

There is still another series of observations and experi-

[1] Virchow's Archives, Bo. Zn. H. II. Experimentelle Untersuchungen über die functionen des Gehirns.

ments on the nerve centres, of an entirely different kind, to which I shall refer. They were made by a Swiss physiologist named Gudden.[1] His method is to mutilate the organs of sense of young animals—say on the first or second day after birth—and afterwards to keep them for a considerable time alive, so as to study the effects of the mutilation on the nervous centres. He states that the operations are wonderfully successful, because the blood of young animals coagulates with great readiness, and the wound invariably heals by first intention. He asserts that a young animal will survive an operation, which would in all probability kill it a few weeks later. This is probably owing to the great energy of tissue growth in young animals. The results obtained by this novel method may be briefly summed up as follows:—

1. Removal of the cerebral hemispheres of the young animal is followed by idiocy in the adult.

2. The organs of voluntary motion are situated in the anterior lobes of the brain—termed by Gudden "psycho-motor centres"—thus agreeing with Fritsch and Hitzig, and also with Ferrier.

3. Removal of these so-called psycho-motor centres on one side, is followed in the adult by atrophy of the opposite and corresponding pyramid of the medulla oblongata.

4. By closing one nasal opening in a young rabbit by permanent satures, Gudden found, after six or eight weeks, that all the olfactory organs on that side were atrophied, while those on the other side were hypertrophied.

5. After removal of the olfactory bulb on one side, there was atrophy of the tractus olfactorius on the same side.

6. Removal of both olfactory bulbs is soon followed by death of the animal, because it is unable to find the mother's breast.

7. On closing the eyes and ears of very young animals, so that these senses were abolished, the animals having to exercise to a great extent the olfactory sense, the olfactory apparatus became hypertrophied.

[1] Experimental untersuchungen über das peripherische und centrale nerven system. Archiv. für psychiatrie und nervenkrankheiten. Bd. II.

8. By destroying the eye on one side, or by simply shutting out light from it for a long period of time by stitching the margins of the eyelids together, the optic nerve and anterior prominence of the corpora quadrigemina on the same side were found atrophied.

9. A blind rabbit uses its ears as organs of touch by movements similar to those made by the antennæ of an insect. The ears consequently become larger, and both muscles and nerves become hypertrophied.

10. When an eye of a pigeon was enucleated soon after the bird was hatched, and the body was examined eight weeks after the operation, atrophy of the corresponding optic nerve, of the corresponding optic lobe, and of the corresponding hemisphere, was observed. When both eyes were enucleated, the bird grew up in a condition of idiocy. "The brain of the operated pigeons, compared with that of the non-operated pigeons, hatched contemporaneously of the same pair, and killed simultaneously, show the following differences in weight:—

| | Weight in Grammes. |
|---|---|
| The brain of non-operated pigeon . . | 1·84 |
| The brain of pigeon blind on one side . | 1·73 |
| The brain of pigeon completely blind . | 1·39" |

These researches show clearly two facts: 1st, The dependence, as regards growth and development, between the organs of sense and their corresponding centres in the brain; and 2d, The fact that, in the pigeon, as I have already pointed out in this paper, the perception of visual impressions is a very important function of the cerebral lobes.

## *IV. THE DEVELOPMENT OF HEAT IN NERVES AND NERVE CENTRES DURING PHYSIOLOGICAL ACTION.*

By means of a delicate thermopile and thermo-galvanometer, Schiff[1] has detected heat in the cerebral hemispheres on the transmission of a stimulus from the periphery of the

[1] Archiv. de Phys. Normal et Pathol., II. and III.

body, and he found that more heat was developed in the middle of the hemispheres than in any other part. He also detected heat in nerves during the transmission of an influence.

These researches are highly valuable, inasmuch as they demonstrate that physical changes occur in the nerves and brain during physiological action.

## *V. THE ACTION OF EXTERNAL MODES OF ENERGY ON THE TERMINAL ORGANS OF THE SENSES.*

The only research which bears upon this point with which we are acquainted, is one undertaken and carried on in the spring of last year by my friend, Mr James Dewar, and myself.[1] The specific object of the inquiry was, if possible, to determine the actual change produced by the action of light on the retina. Numerous hypotheses have been made from time to time by physicists and physiologists ; but up to the present date our knowledge of the subject is without any experimental foundation. For example, Newton, Melloni, and Seebeck, stated that the action of light on the retina consisted of a communication of mere vibrations; Young conjectured that it was a minute intermittent motion of some portion of the optic nerve; Du Bois-Reymond attributed it to an electrical effect; Draper supposed that it depended

[1] Since the above was written, it has come to our knowledge that the subject of the action of light on the retina had been investigated previous to the publication of our paper, by H. Fr. Holmgren, a distinguished Swedish physiologist. We have read his papers published in the "Upsala Lakereförenings Förhandlingar." It was with pleasure we at once acknowledged that he has the claim of priority in observing an electrical fluctuation by the action of light, and that his memoirs were valuable contributions to science. It is, however, almost needless to state that our work was done in entire ignorance of any previous observations on the subject, and that our methods of experiments, the delicacy of our instrument, and the distinct numerical data obtained, have enabled us to prosecute the matter in various new directions. Great interest is now felt in the subject by continental physiologists, and the matter has been taken up by Du Bois-Reymond, Valentin, and Donders.

on a heating effect of the choroid; and Mosier compared it to the action of light on a sensitive photographic plate.

It is evident that, in accordance with the principle of the transference of energy now universally accepted, the action of light on the retina must produce an equivalent result, which may be expressed, for example, as heat, chemical action, or electro-motive power. It is well known that the electro-motive force of a piece of muscle is diminished when it is caused to contract by its normal stimulus, the nervous energy conveyed along the nerve supplying it; and similarly a nerve suffers a diminution of its normal electro-motive force during action. In the same manner, the amount and variations of the electro-motive power of the optic nerve affected secondarily by the action of light on the retina, are physical expressions of certain changes produced in the latter; or, in other words, are functions of the external exciting energy, which in this case is light. Considerations such as these led us to form the opinion that the problem of what effect, if any, the action of light has on the electro-motive force of the retina and optic nerve, would require for its investigation very careful and refined experiment.

The inquiry divided itself into two parts,—first, to ascertain the electro-motive force of the retina and nerve; and, second, to observe whether this was altered in amount by the action of light. The electro-motive force of any living tissue can be readily determined by the method of Du Bois-Reymond. This great physiologist found that every point of the external surface of the eyeball of a large tench was positive to the artificial transverse section of the optic nerve, but negative to the longitudinal section. This he accomplished by the use of his well-known non-polarizable electrodes, formed of troughs of zinc carefully amalgamated, containing a solution of neutral sulphate of zinc, and having cushions of Swedish filter paper on which to rest the preparation. (To protect the preparation from the irritant action of the sulphate of zinc, a thin film or guard of sculptor's clay, moistened with a ·75 per cent. solution of common salt, and worked out to a point, is placed on each cushion.) These electrodes were connected with a galvanometer, and the preparation was placed so that the eyeball, carefully freed from muscle, rested on the one clay-guard, while the transverse section of the optic nerve was in contact with the other. By following Du Bois-Reymond's method, we have had no difficulty in obtaining a strong deflection from the eyes of rabbits, cats, dogs, pigeons, an owl, a tortoise, numerous frogs and toads, a serpent, gold fish, stickleback, rockling, and various species of crustaceans. The deflection was frequently so much as to drive the spot of light off the galvanometer scale.

With regard to the second question—namely, Whether, and to what extent, the electro-motive force would be effected by light? we found more difficulty. The method followed was to place the eyeball on the cushions in the manner above described, to note the deflection of the galvanometer needle, and then to observe whether or not any effect was produced on the impact of a beam of light, during its continuance, and on its removal. In a few of our earlier experiments we used Du Bois-Reymond's multiplying galvanometer, but finding the amount of deflection obtained was so small that the effect of light could not be readily observed, we have latterly used Sir W. Thomson's exceedingly sensitive reflecting galvanometer, kindly lent us by Professor Tait. We met also with secondary difficulties, such as the dying of the nerve, the impossibility of maintaining an absolutely constant zero, and an absolutely constant amount of polarity, the effects of heat, &c.; but these difficulties we have overcome as far as possible by the most approved methods. The changes in polarity of the apparatus occurred slowly, and could not be mistaken for the changes produced by the action of light, which we found occurred suddenly, and lasted a short period of time. It is also important to state that the deflections we observed do not at present profess to be absolute, but only relative values. About five hundred observations were made in this research, and we took every precaution to obtain accurate results. The effects of heat were carefully avoided, by covering over the troughs, on which the eye under examination rested, with a spherical doubleshell of glass, having at least an inch of water between the walls.

The results we have arrived at are as follows :—

1. The action of light on the retina is to alter the amount of the electro-motive force to the extent of from 3 to 7 per cent. of the total amount of the natural current.

2. A flash of light, lasting the fraction of a second, produces a marked effect.

3. A lighted match, held at a distance of four or five feet, is sufficient to produce an effect.

4. The light of a small gas flame enclosed in a lantern, and caused to pass through a globular glass jar (12 inches in diameter), filled with a solution of ammoniacal sulphate of copper or bichromate of potash, has also produced a change in the amount of the electro-motive power.

5. The action of light on the eye of the frog is as follows :— When a diffuse light is allowed to impinge on the eye of the frog, after it has arrived at a tolerably stable condition, the natural electro-motive power is in the first place increased, then diminished ; during the continuance of light, it is still slowly diminished to a point where it remains constant; and on the removal of light, there is a sudden increase of the electro-motive power nearly up to its original position. The alterations above referred to are variables, depending on the quality and intensity of the light employed, the position of the eyeball on the cushions, and modifications in the vitality of the tissues.

6. Similar experiments made with the eye of warm-blooded animals, placed on the cushions as rapidly as possible after the death of the animal, and under the same conditions, have never given us an initial positive variation, as we have above detailed in the case of the frog, but always a negative variation. The after inductive effect on the withdrawal of light occurs in the same way.

7. Many experiments have been made as to effect of light from different portions of the spectrum. This was accomplished by causing different portions of the spectrum of the oxy-hydrogen lime-light to impinge on the eye. All these

observations tend to shew that the greatest effect is produced by those parts of the spectrum that appear to consciousness to be the most luminous; namely, the yellow and the green.

## CONCLUSION.

In conclusion, I have to say that time will not permit me to refer to the elaborate researches which have been made as to the functions of individual nerves, such as the vagus, chorda tympani, &c., &c. I have rather attempted to give an account of the advances in our knowledge of the nerve centres, which have recently been so marked. Finally, let me allude to the fact that psychical phenomena are at present being investigated experimentally in four different ways:—

*First.* By local chemical irritations applied to limited areas on the surface of the brain, as illustrated by the method of Nothnagel.

*Second.* By direct galvanic or faradic stimulation of areas on the surface of the brain, as pursued by Fritsch and Hitzig, and by Ferrier.

*Third.* By operating on the organs of sense at birth, and noting any change in the form, texture, weight, and appearance of the corresponding nervous centres in adult life, as practised by Gudden; and,

*Fourth.* By observing and registering the specific effect of external modes of energy on the terminal organs of the senses,—such as of light on the retina, sound on the internal ear and rods of Corti, sapid substances on the taste-organs of the tongue, odoriferous particles on the olfactory membrane, and contact with the touch-organs of the skin. This is the inquiry at present being carried on by Mr Dewar and myself.

When the knowledge gained by the pursuit of these modes of research is added to that still to be derived from clinical and pathological observation, it is not a vain hope that before many years the physiology of the great nervous centres will be better understood than it is at present.